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ABSTRACT

Cover crops are important components of a sustainable crop-production system in plantation crops such as cacao (*theobroma cacao*), coffee (*Coffee arabica*), oil palm (*Elaeis Spp.*), and banana (*Musa Spp.*). Optimal growth of cover crops in plantation agriculture is determined by adaptability of crop species, light intensity reaching their leaf canopies, and their nutrient-use efficiencies, including those of micronutrients. An experiment was conducted in a climatically controlled growth chamber to evaluate the influence of levels of light intensity on growth and micronutrient [boron (B), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn)] uptake parameters in legume cover crops. Two photosynthetic photon flux density (PPFD, 200 and 400 μmol m^{-2} s^{-1}) light treatments were imposed on nine legume species (joint vetch (*Aeschynomene americana*), sunhemp (*Crotalaria juncea* L.), *Crotalaria rchroleuca*, showy crotalaria (*crotalaria spectabilis*), hairy indigo (*Indigofera hirsute* L.), lab-lab (*Lablab purpureus*), sesbania (*Sesbania microcarpa*), Brazilian stylo (*Stylosanthes guianensis*), and cowpea (*Vigna unguiculata*)). Overall, light intensity significantly affected growth, micronutrient uptake, and use-efficiency ratios; with few exceptions, interactions between cover crop species and PPFD were also significant. Such PPFD $\times$ crop species interactions show that the cover crops used in this study differed in growth and nutrient-uptake parameters under the conditions imposed. Sunhemp, cowpea, sesbania, and lab-lab species were superior in producing shoot dry weight and in nutrient accumulation compared with other species at lower as well as at higher PPFD levels. Interspecific differences in nutrient influx and

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transport were observed. Influx and transport of micronutrients was in the order Mn > B > Fe > Zn > Cu. Overall, growth, nutrient uptake, and use-efficiency ratios were higher at higher PPFD than at lower PPFD. Results of this study indicate that the use of proper crop species at adequate light intensities is an important component of successful cultivation of cover crops in plantation agriculture.

Keywords: nutrient transport, nutrient flux, nutrient efficiency ratio, root and shoot weight

INTRODUCTION

Cover crops can be important components of a sustainable crop-production system in widely spaced plantation crops such as cacao, coffee, oil palm, rubber, and banana. In plantation crops, the soil is unprotected, especially during early-growth stages, and is subjected to loss by erosion. Weed infestation is also a serious problem in the early-growth stage of plantation crops. Inclusion of fast-growing cover crops in the early stages of plantation-crop establishment could help to reduce soil erosion and nutrient leaching and increase organic-matter buildup leading to restoration of soil productivity (Cunningham and Smith, 1961; Wood and Lass, 2001).

The beneficial effect of legume cover crops in rotation with field crops has long been recognized (Smith et al., 1987; Blevins and Frye, 1993). Cover crops reduce soil erosion, increase water infiltration, improve soil tilth, minimize leaching losses of nutrients, help to conserve moisture, and control weeds (Blevins and Frye, 1993; McCracken et al., 1994; Reicosky and Forcella, 1998; Sustainable Agriculture Network, 1998).

Cover crops are grown in plantation systems as understory plants; hence, they do not receive full sunlight. Cover crops that tolerate low light intensity will have greater impacts on soil fertility and productivity of plantation crops than those requiring higher light intensities. Saturating photosynthetic photon flux density (PPFD) for photosynthesis in cacao (*theobroma cacao*) has been reported to be around 400 μmol m^{-2} s^{-1} (Raja Harun and Hardwick, 1987). Therefore, shade trees are planted along with cacao to reduce the intensity of light reaching the cacao-leaf canopy. In cacao plantations, a PPFD of around 400 μ mol m^{-2} s^{-1} near the cacao leaf canopy is achieved by controlling the number of shade trees and by pruning. Canopies of shade trees and cacao together reduce the amount of PPFD at the cover-crop canopy levels. Tropical soils under plantation crops generally have low fertility, including law levels of micronutrients. Productivity and persistence of cover crops in tropical plantation crops is therefore greatly influenced by light intensity at ground level and by the level of soil fertility.

In the tropics, increasing crop productivity and maintaining a clean environment are major challenges to agricultural scientists in the twenty-first century. With proper selection, use, and management, it is possible to improve the persistence and productivity of these cover crops, which will lead to enhanced soil fertility and improved sustainability of plantation crops. Limited numbers of legume crops, such as cacao, have been tested for their suitability as cover crops in plantation agriculture (Jordan and Opoku, 1966; Opoku, 1970; Wilson, 1999; Wood and Lass, 2001). However, large numbers of legume cover crops exist that may be tolerant to tropical abiotic stresses such as low soil pH, low levels of soil nutrients, high temperatures, and drought (Duke, 1981; Wessel and Maesen, 1997). Such plants may be useful as potential cover crops for plantation systems. Cover crops can improve soil quality factors—such as physical, chemical, and biochemical properties—and add to environmental benefits. Yet the adoption of cover crops into plantation management has been limited. Furthermore, information is scarce concerning the suitability of begumes as a cover crop and their ability to grow as understory plants under the reduced light intensities common in plantation systems. An experiment was conducted under controlled conditions, with the objective of evaluating the influences of two PPFDs, (200 and 400 μmol m^{-2} s^{-1}) on the growth, micronutrient uptake, and use efficiencies of nine tropical legume cover crops.

MATERIALS AND METHODS

Growth Medium, Seeds, and Seedling

Various cover crop seeds were planted in one-gallon black plastic containers containing 2 kg of perlite: sand: promix (2:2:1 volume basis). Fertilizers were added to the growth medium to provide (mg/kg) 600 nitrogen (N), 600 phosphorus (P), 240 potassium (K), 1012 calcium (Ca), 309 magnesium (Mg), 500 sulfur (S), 119 iron (Fe), 0.7 boron (B), 17.5 manganese (Mn), 7.0 copper (Cu), 7.0 zinc (Zn), and 0.35 molybdenum (Mo). Nine annual erect shrub-type leguminous cover crops were used in this study (Table 1). These include: 1. joint vetch (*Aeschynomene americana*), 2. sunhemp/Indian hemp (*Crotalaria juncea* L.), 3. crotalaria ochroleuca (*Crotalaria orchroleuca*), 4. showy crotalaria (*Crotalaria spectabilis*), 5. hairy indigo (*Indigofera hirsute* L), 6. Lab-lab (*Lablab purpureus*), 7. sesbania (*Sesbania microcarpa*), 8. Brazilian lucerne/Brazilian stylo (*Stylosanthes guianensis*), and 9. cowpea/Fejao caupi (*Vigna unguiculata*). Seeds were received from various sources: seeds of 1 and 5 were received from Adams-Briscoe Seed Co., Jackson, GA; 2, 3, 4, and 6 were received from the Pirai seed company, Piracicaba, Brazil; seeds of 7 were received from Dr Y. Li TREC of the University of Florida, Homestead, FL; seeds of 8 were received from the Globo rural seed company, Goania, Brazil; and seeds of 9 were received from Dr. Corival da Silva of the Embrapa Rice and Bean Center, GO Brazil. For each pot, 5–20 seeds (depending on the seed size) of each cover crop were planted at 2–3 cm depth, covered with growth medium, and watered to field capacity. On the tenth day of growth, plants in each pot were thinned to

Table 1
Influence of photosynthetic photon flux density (PPFD) on concentration (μg/g) of micronutrients in nine species of leguminous cover crops

Crop species	PPFD[†]	B	Cu	Fe	Mn	Zn
1. Joint vetch	L_1	41	33	213	494	82
	L_2	36	32	132	295	79
2. Sunhemp	L_1	53	17	101	424	54
	L_2	45	18	135	456	57
3. Crotalaria ochro	L_1	60	23	109	570	50
	L_2	48	17	103	432	52
4. Showy crotalaria	L_1	51	23	91	333	58
	L_2	48	24	104	261	62
5. Hairy indigo	L_1	47	29	88	175	56
	L_2	59	41	80	187	57
6. Lab-lab	L_1	40	38	138	331	99
	L_2	32	103	142	203	75
7. Sesbania	L_1	41	26	117	289	73
	L_2	41	32	102	219	51
8. Brazilian stylo	L_1	25	18	73	162	62
	L_2	25	20	82	86	49
9. Cowpea	L_1	34	12	156	451	101
	L_2	22	10	111	360	76
Mean	L_1	43	24	121	359	71
	L_2	40	33	110	278	62
Significance						
Species (S)		**	NS	**	**	**
PPFD (P)		*	NS	NS	**	**
S × P		*	NS	NS	NS	**

[†]L_1 = PPFD of 200 μmol m^{-2} s^{-1} and L_2 = 400 μmol m^{-2} s^{-1}.
[*,**,NS]Significant at 5% and 1% probability level and nonsignificant, respectively.

two/pot for large-growing species and seven/pot for smaller-growing species. Seedlings removed at this initial harvest were used to determine initial growth and nutrient-uptake parameters.

Growth Conditions

Plants were grown in a climatically controlled growth room. An EGC (Environmental Growth Chambers, Chagrin Falls, OH, Model GR-48) growth room was used. Day temperature was 30°C at 75% relative humidity and night temperature was 28°C at 75% relative humidity. Plants were grown (14 h) at two PPFDs, 200 μmol m^{-2} s^{-1} and 400 μmol m^{-2} s^{-1}. These two levels of PPFD were selected mainly because saturating PPFD for cacao is between 200 and 400 μmol m^{-2} s^{-1}(Raja Harun and Hardwick, 1987) The main growth chamber was maintained at 400 μmol m^{-2} s^{-1}. Within the growth room, a mini chamber was constructed with 2 cm diameter PVC pipe and covered with various layers of plastic shade cloth to achieve 200 μmol m^{-2} s^{-1} of PPFD. Every other day, pots were weighed and the desired amount of deionized water was added to maintain soil water levels at field capacity.

Observations

After three months of growth, roots and shoots were separated and washed with deionized water. Leaves were separated and leaf area was determined with a Li-Cor model 300 leaf area meter (Li-Co., Lincoln, NB). Roots and shoots were dried at 70°C for 5 d and dry weights were recorded. Shoot samples were ground to pass a 0.55 mm mesh sieve. Chemical analysis of the shoot samples was performed at the A & L Southern Agricultural Lab, Pompano Beach, FL, by adapting a modified method suggested by Wolf (1982).

Nutrient influx (IN), nutrient transport (TR), and nutrient use efficiency (ER) parameters were calculated using the following equations:

$$\mathrm{IN} = [(\mathrm{U}_2 - \mathrm{U}_1)/(\mathrm{T}_2 - \mathrm{T}_1)] \times [(\ln \mathrm{Wr}_2 - \ln \mathrm{Wr}_1)/(\mathrm{Wr}_2 - \mathrm{Wr}_1)]$$

where U refers to elemental content of shoot (micromoles/plant), T refers to time in seconds, Wr refers to root weight (grams/plant), and subscripts 1 and 2 refer to initial and final harvest times;

$$\mathrm{TR} = [(\mathrm{U}_2 - \mathrm{U}_1)/(\mathrm{T}_2 - \mathrm{T}_1)] \times [(\ln \mathrm{Ws}_2 - \ln \mathrm{Ws}_1)/(\mathrm{Ws}_2 - \mathrm{Ws}_1)]$$

where Ws refers to shoot weight (g/plant);

and

$$\mathrm{ER} = [\text{mg of Ws/mg of any given element in shoot}]$$

Treatments were replicated three times and data were subjected to analysis of variance using the general linear model (GLM) procedures of SAS (Ver. 8, SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Shoot and Root Growth

Crop species × light intensity (PPFD) interactions for shoot dry weight were highly significant ($P \leq 0.01$), indicating that the crop species responded

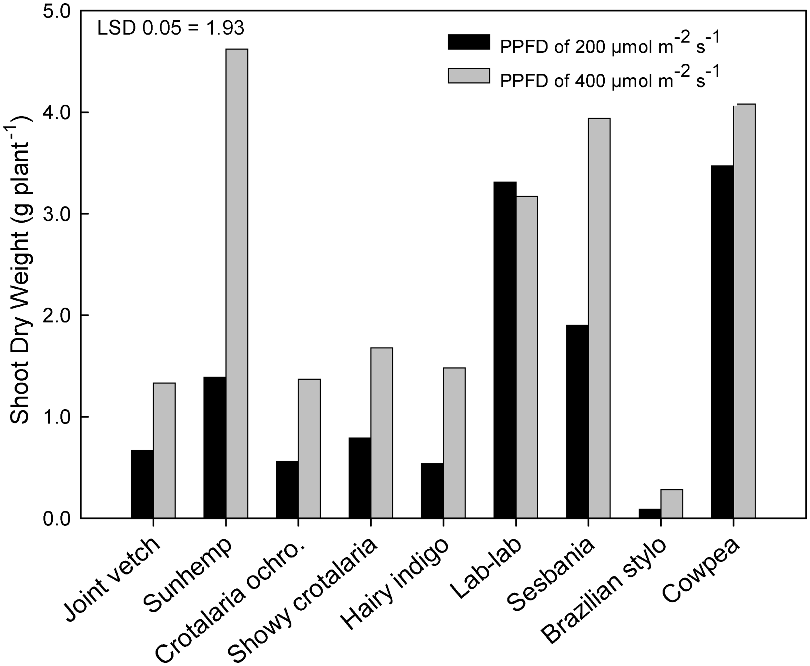

Figure 1. Relationship between shoot dry weight and PPFD of legume cover crops.

differently to PPFD. All crop species produced higher shoot yield at 400 μmol m^{-2} s^{-1} than at 200 μmol m^{-2} s^{-1} PPFD, except lab-lab (Figure 1). Across all species, shoot dry weight was increased 73% at 400 μmol m^{-2} s^{-1} compared with 200 μmol m^{-2} s^{-1} PPFD. Maximum shoot weight was produced by sunhemp, followed by cowpea and sesbania at 400 μmol m^{-2} s^{-1} PPFD. The increase in shoot weight of sunhemp was 232%, that of cowpea was 18%, and that of sesbania was 107% at 400 μmol m^{-2} s^{-1} PPFD compared with 200 μmol m^{-2} s^{-1} PPFD. Lab-lab and cowpea produced good shoot weights at lower as well as at higher light intensities, which indicated that both were suitable as cover crops at both light intensities. Lowest shoot dry weight was produced by Brazilian stylo followed by joint vetch, crotalaria ochroleuca, hairy indigo, and showy crotalaria at 400 μmol m^{-2} s^{-1} PPFD. These five species also produced the lowest shoot dry weights at 200 μmol m^{-2} s^{-1} PPFD. The higher shoot weights of sunhemp, cowpea, and lab-lab appeared to be associated with their high leaf areas at both PPFD levels (Figure 2). With higher leaf areas, these crops might have higher photosynthetic rates than other plant species. Moss (1984) reported that plants with large leaf areas have a potential for greater growth than those with smaller leaf areas. But sesbania had a smaller leaf area and still produced good shoot growth. This result

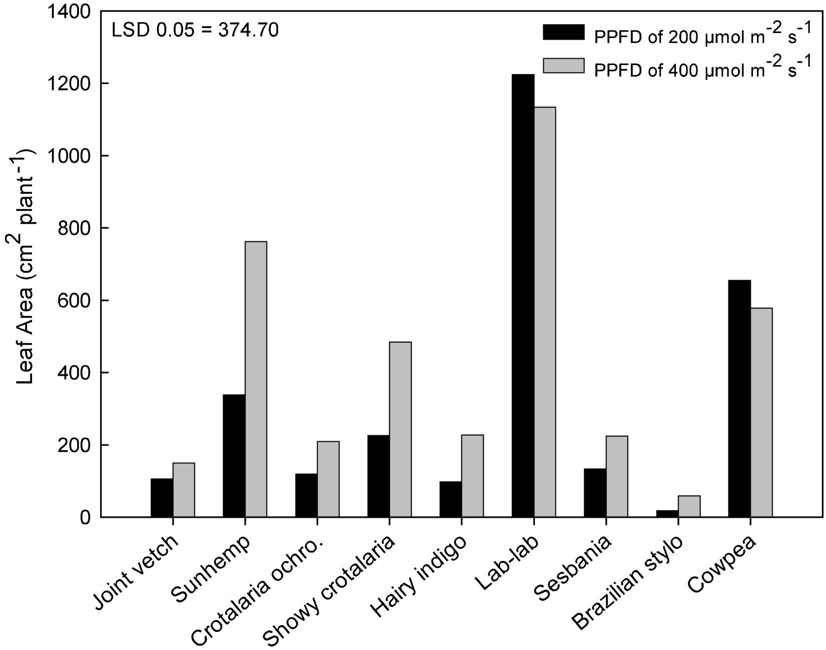

Figure 2. Relationship between leaf area and PPFD of legume cover crops.

indicated that this species might have a higher photosynthetic rate even with a smaller leaf area than the other plant species tested. Sesbania had greater height (data not shown) than other crop species, and this growth tendency might have helped it to produce higher photosynthesis due to less mutual shading of leaves. Brown (1984) reported that height is an important characteristic and benefits the plant by having the most efficient leaves in the most favorable position for photosynthesis.

Crop species significantly ($P \leq 0.05$) affected root dry weight (Figure 3). Higher root weight species may be able to absorb more water and nutrients by exploring larger volumes of soil and thus may be better adapted as cover crops. This is true only when environmental conditions are not favorable. Under optimum conditions (for water and nutrients) a smaller root system is generally sufficient to supply the needs of the plants (Brown, 1984). With the exception of lab-lab and Brazilian stylo, root dry weight increased with increasing PPFD (Figure 3). Across crop species, the high light-intensity treatment (400 μmol m^{-2} s^{-1}) produced 62% higher root weights than did the lower light intensity one (200 μmol m^{-2} s^{-1}). The PPFD $\times$ crop species interactions for root weight were not significant, which indicated consistent differences in crop species root weight at both light intensities.

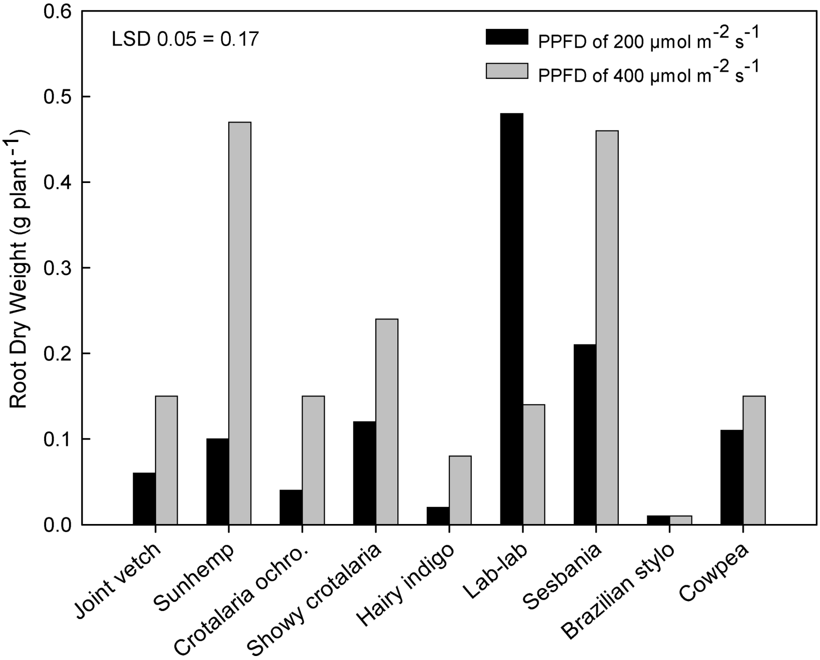

Figure 3. Relationship between root dry weight and PPFD of legume cover crops.

Micronutrient Concentration and Uptake

Concentrations of micronutrients, except for Cu in shoots, were highly significantly ($P \leq 0.01$) influenced by crop species (Table 1). Similarly, light intensity significantly influenced micronutrient concentrations, except of Cu and Fe. Crop species × PPFD interactions were significant only for B and Zn (Table 1). Across the nine crop species, concentrations of all the micronutrients were higher at the lower light intensity (200 μmol m^{-2} s^{-1} PPFD) than at the higher light intensity (400 μmol m^{-2} s^{-1}PPFD), except for Cu. However, overall Cu concentrations tended to increase with increasing PPFD. The decrease in concentration with increased light intensity was B, 8%; Fe, 10%; Mn, 29%; and Zn, 15% at 400 μmol m^{-2} s^{-1} PPFD compared with 200 μmol m^{-2} s^{-1} PPFD. The decrease in most of the micronutrient concentrations at higher light intensity was probably associated with higher dry weights of shoots achieved at this light level. Such an effect is known as the dilution factor in mineral nutrition (Jarrell and Beverly, 1981). Overall concentrations of micronutrients were in the order of Mn > Fe > Zn > B > Cu. Fageria et al. (2002) and Bennett (1993) reported a similar pattern of micronutrient concentrations in other species of crop plants. Mengel et al. (2001) stated that Cu is taken up by the plants in very small quantities because the Cu requirement of crop plants is relatively low.

Uptake of micronutrients was significantly ($P \leq 0.05$) affected by crop species and PPFD (Table 2). Similarly, species × PPFD interactions were highly significant for all the micronutrients except B. Crop species × light interaction indicates variation in micronutrient uptake among crop species at the two light levels. Lab-lab, cowpea, sesbania, and sunhemp accumulated greater amounts of micronutrients at both PPFD levels; this is a reflection of maximum shoot dry-matter production by these species. At both PPFD levels, Brazilian stylo produced minimum dry matter and hence accumulated minimum amounts of micronutrients in the shoot. Interspecific variation in micronutrient accumulation has been reported for legumes (Fageria et al., 2002). Micronutrient

Table 2

Influence of photosynthetic photon flux density (PPFD) on uptake (μg/plant) of micronutrients in nine species of leguminous cover crops

Crop species	PPFD†	B	Cu	Fe	Mn	Zn
1. Joint vetch	L_1	27.74	22.08	135.79	327.72	54.49
	L_2	48.70	43.27	178.99	393.35	106.04
2. Sunhemp	L_1	75.89	23.75	137.38	629.18	75.96
	L_2	207.52	81.84	612.17	2114.90	260.55
3. Crotalaria ochro	L_1	33.30	12.95	60.92	316.15	27.47
	L_2	67.09	23.77	141.68	587.52	71.10
4. Showy crotalaria	L_1	39.67	17.92	71.68	260.21	45.64
	L_2	79.14	39.50	174.61	438.93	103.60
5. Hairy indigo	L_1	25.63	15.66	47.23	97.25	30.45
	L_2	85.66	61.98	111.75	269.69	84.15
6. Lab-lab	L_1	131.55	125.88	458.43	1102.07	332.53
	L_2	103.82	291.12	450.80	655.42	234.79
7. Sesbania	L_1	80.07	49.24	208.93	511.54	138.55
	L_2	159.34	122.15	401.27	865.01	200.09
8. Brazilian stylo	L_1	2.32	1.67	6.76	15.00	5.74
	L_2	7.04	5.45	22.59	23.83	13.48
9. Cowpea	L_1	116.91	42.76	529.45	1567.13	350.21
	L_2	91.84	41.72	458.72	1465.80	310.96
Mean	L_1	59.23	34.66	184.06	536.25	117.90
	L_2	94.46	78.98	283.62	757.16	153.86
Significance						
Species (S)		**	**	**	**	**
PPFD (P)		*	**	**	**	**
S × P		NS	**	**	**	**

†L_1 = PPFD of 200 μmol m^{-2} s^{-1} and L_2 = 400 μmol m^{-2} s^{-1}.

*,**,NS Significant at 5% and 1% probability level and nonsignificant, respectively.

accumulation across nine crop species was higher with high PPFD than with lower PPFD. Across all legume species increasing PPFD from 200 to 400 μmol m^{-2} s^{-1} increased accumulation (μg/plant) of B by 59%, Cu by 128%, Fe by 54%, Mn by 41%, and Zn by 30%. The accumulation of micronutrients in plants is of interest because of the possible relationship between yield and nutrient accumulation (Rasmusson and Gengenbach, 1984). Atkinson (1990) reported that a plant's demand for a nutrient is related to its biomass production and its rate of uptake is related to its growth rate. As biomass production increases, the demand for nutrients, both the total amount and the intensity of uptake, increases. The overall micronutrient accumulation pattern in the current study was in the order of Mn $>$ Fe $>$ Zn $>$ B $>$ Cu. This trend was similar to that observed for the micronutrient concentrations. Overall, micronutrient uptake was significantly and positively correlated with both shoot and root dry weight. Correlations between shoot dry weight and micronutrient uptake were B, 0.92** (** refers to significant at 0.001 level of probability); Cu, 0.39**; Fe, 0.92**; Mn, 0.90**; and Zn, 0.92**. Whereas, correlations between root dry weight and micronutrient uptake were B, 0.60**; Cu, 0.29**; Fe, 0.54**; Mn, 0.41**; and Zn, 0.41**. The positive association between nutrient uptake and shoot and root dry weights indicate an increase in nutrient uptake with increasing shoot and root biomass accumulation. Higher correlation between shoot dry weights versus micronutrient uptake compared with root dry weight versus micronutrient uptake indicates that shoot weight had a greater influence on micronutrient uptake.

Micronutrient Flux and Transport

Nutrient flux (uptake in shoot per unit root weight per unit time) was significantly ($P \leq 0.05$) affected by crop species (Table 3). However, PPFD did not significantly influence nutrient flux rates, except for that of Mn, which was generally decreased with increasing PPFD. There was no significant effect of crop species $\times$ PPFD on micronutrient influx. Such nutrient flux behavior may be associated with root weight, which was affected significantly only by crop species treatment (Figure 3). With one exception, Cu, the overall influx of B, Fe, Mn, and Zn was lower at higher PPFD than at lower PPFD. This result is associated with higher root weight at higher light intensity compared with lower light density. Across nine crop species, root weight increases were 62% greater at higher PPFD than at lower PPFD (Figure 3). Variation for root-system morphology has been shown within legume species (Atkinson, 1990; Caradus, 1990). Such differences in root morphology might have contributed to variations in micronutrient influx rates among different legume cover crops.

Transport of B, Cu, Fe, Mn, and Zn into shoots (amount of nutrient transported in shoots per unit shoot weight per unit time) was significantly ($P \leq 0.05$) influenced by crop species (Table 4). PPFD significantly ($P \leq 0.01$) decreased transport only of Mn. Overall, an increase in PPFD slightly increased the

Table 3
Influence of photosynthetic photon flux density (PPFD) on influx rate (pmol/g root/sec) of micronutrients in nine legume cover crops

Crop species	PPFD†	B	Cu	Fe	Mn	Zn
1. Joint vetch	L_1	71.54	9.73	70.71	168.56	23.47
	L_2	53.98	8.20	37.35	86.76	19.39
2. Sunhemp	L_1	63.38	3.41	23.05	101.83	10.63
	L_2	55.68	3.72	32.31	112.37	11.68
3. Crotalaria ochro	L_1	96.76	6.28	34.27	181.41	13.19
	L_2	70.15	4.25	28.79	122.55	12.33
4. Showy crotalaria	L_1	47.34	3.60	16.73	60.20	8.92
	L_2	45.01	3.82	19.37	48.67	9.69
5. Hairy indigo	L_1	146.50	15.31	52.21	109.60	28.83
	L_2	184.91	21.44	45.75	111.75	29.92
6. Lab-lab	L_1	92.24	14.55	60.80	172.36	41.60
	L_2	57.38	21.16	47.82	70.59	21.29
7. Sesbania	L_1	57.21	6.04	29.58	78.87	16.56
	L_2	61.10	8.00	29.79	65.26	12.68
8. Brazilian stylo	L_1	46.17	5.68	26.25	58.64	19.13
	L_2	57.16	7.56	35.88	37.68	18.16
9. Cowpea	L_1	78.55	4.69	73.39	213.29	39.98
	L_2	41.26	3.00	41.38	138.19	24.27
Mean	L_1	77.74	7.70	43.00	127.20	22.48
	L_2	69.63	9.02	35.38	88.20	17.71
Significance						
Species (S)		**	**	**	**	*
PPFD (P)		NS	NS	NS	*	NS
S × P		NS	NS	NS	NS	NS

†L_1 = PPFD of 200 μmol m^{-2} s^{-1} and L_2 = 400 μmol m^{-2} s^{-1}.
*,**,NS Significant at 5% and 1% probability level and nonsignificant, respectively.

transport of B and Cu, and slightly decreased the transport of Fe, Mn, and Zn. Similarly, the crop species × PPFD interaction was significant ($P \leq 0.05$) for transport of B, Mn, and Zn. Micronutrient rate of transport to the shoot was in the order Mn > B > Fe > Zn > Cu. Inter- and intraspecific differences in nutrient influx and transport have been related to differences in shoot demand per unit of nutrient absorbed (Devine et al., 1990; Baligar et al., 2001; Gerloff and Gabelman, 1983).

Micronutrient Use Efficiency

Nutrient use efficiency ratio (ER) for micronutrients was significantly ($P \leq 0.05$) influenced by crop species treatment (Table 5). However, PPFD

Table 4
Influence of photosynthetic photon flux density (PPFD) on transport rate (pmol/g shoot/sec) of micronutrients in nine legume cover crops

Crop species	PPFD†	B	Cu	Fe	Mn	Zn
1. Joint vetch	L_1	6.80	0.93	6.78	16.11	2.24
	L_2	6.31	0.96	4.46	10.09	2.28
2. Sunhemp	L_1	6.18	0.33	2.25	9.88	1.03
	L_2	6.46	0.43	3.76	13.02	1.35
3. Crotalaria ochro	L_1	8.79	0.57	3.11	16.52	1.20
	L_2	7.92	0.48	3.27	13.90	1.40
4. Showy crotalaria	L_1	6.94	0.53	2.39	8.92	1.31
	L_2	6.89	0.58	2.92	7.43	1.48
5. Hairy indigo	L_1	8.05	0.84	2.90	5.90	1.58
	L_2	11.11	1.32	2.87	6.92	1.78
6. Lab-lab	L_1	4.14	0.68	2.82	6.82	1.73
	L_2	3.46	1.87	2.98	4.26	1.33
7. Sesbania	L_1	2.17	0.75	3.86	9.61	2.08
	L_2	8.04	1.08	3.90	8.55	1.66
8. Brazilian stylo	L_1	2.92	0.36	1.66	3.71	1.21
	L_2	3.73	0.49	2.35	2.46	1.19
9. Cowpea	L_1	3.19	0.19	2.91	8.61	1.61
	L_2	2.12	0.16	2.13	7.01	1.24
Mean	L_1	5.46	0.58	3.19	9.56	1.55
	L_2	6.23	0.82	3.18	8.18	1.52
Significance						
Species (S)		**	*	**	**	**
PPFD (P)		NS	NS	NS	**	NS
S × P		*	NS	NS	*	**

†L_1 = PPFD of 200 μmol m^{-2} s^{-1} and L_2 = 400 μmol m^{-2} s^{-1}.
*,**,NS Significant at 5% and 1% probability level and nonsignificant, respectively.

and crop species × PPFD significantly ($P \leq 0.01$) influenced nutrient-use efficiency ratios only for B, Mn, and Zn. This result indicates that B, Mn, and Zn use efficiency varied with varying light intensity in tropical legumes. Across the nine crop species, the increases in nutrient-use efficiency ratios were B, 14%; Cu, 2%; Fe, 4%; Mn, 31%; and Zn, 10% at 400 μmol m^{-2} s^{-1} PPFD compared with 200 μmol m^{-2} s^{-1} PPFD. Deficiencies of Zn, B, and Fe have been reported for field-grown cacao (Wood and Lass, 2001). This finding indicates that soils under cacao were deficient in these nutrients. Plants having high ER values for these micronutrients might produce higher yield when grown on infertile soils where supplies of these nutrients are limited. Interspecific variation in mineral uptake and utilization in various plant species is well documented (Devine et al., 1990; Baligar et al., 2001; Gerloff and Gabelman, 1983; Vose, 1984). Variations

Table 5
Influence of photosynthetic photon flux density (PPFD) on nutrient efficiency ratio (mg shoot/mg $\times 10^4$ of element in shoot) of micronutrients in nine species of leguminous cover crops

Crop species	PPFD†	B	Cu	Fe	Mn	Zn
1. Joint vetch	L_1	2.45	3.04	0.53	0.20	1.22
	L_2	2.79	3.16	0.84	0.35	1.27
2. Sunhemp	L_1	1.92	5.94	0.99	0.25	1.85
	L_2	2.25	5.69	0.81	0.22	1.79
3. Crotalaria ochro	L_1	1.68	4.48	0.92	0.18	2.04
	L_2	2.08	5.77	0.97	0.23	1.93
4. Showy crotalaria	L_1	1.98	4.38	1.10	0.30	1.72
	L_2	2.13	4.25	0.97	0.39	1.63
5. Hairy indigo	L_1	2.14	3.52	1.14	0.62	1.79
	L_2	1.73	2.53	1.34	0.54	1.76
6. Lab-lab	L_1	2.52	2.67	0.73	0.32	1.03
	L_2	3.14	2.40	0.70	0.50	1.34
7. Sesbania	L_1	2.51	4.06	0.89	0.43	1.39
	L_2	2.67	3.46	0.98	0.46	1.97
8. Brazilian stylo	L_1	4.00	5.56	1.37	0.62	1.61
	L_2	3.97	5.09	1.22	1.16	2.06
9. Cowpea	L_1	2.97	8.19	0.69	0.22	1.00
	L_2	4.52	10.40	0.91	0.28	1.32
Mean	L_1	2.46	4.65	0.93	0.35	1.52
	L_2	2.81	4.75	0.97	0.46	1.67
Significance						
Species (S)		**	**	**	**	**
PPFD (P)		**	NS	NS	**	**
S × P		**	NS	NS	**	**

†L_1 = PPFD of 200 μmol m^{-2} s^{-1} and L_2 = 400 μmol m^{-2} s^{-1}.
*,**,NS Significant at 5% and 1% probability level and nonsignificant, respectively.

in nutrient utilization within and between plant species are known to be under genetic and physiological control but are modified by plant interactions with environmental variables (Devine et al., 1990; Vose, 1984; Baligar and Fageria, 1997; Streeter and Barta, 1984).

CONCLUSIONS

Levels of PPFD had a significant influence on shoot dry weight but response varied according to species. Therefore, selection of cover-crop species that could grow as understory plants in plantation crops such as cacao, coffee, rubber, and banana is possible. Cover crops that tolerate low PPFD could improve soil conservation and soil fertility under plantation crops. Maximum shoot weight was produced by sunhemp, cowpea, lab-lab, and sesbania at 400 μmol m^{-2} s^{-1} of PPFD. Lab-lab appeared to be a good cover crop because it produced good shoot dry matter at lower as well as at higher PPFD. Sunhemp, cowpea, sesbania, and lab-lab accumulated maximum amounts of micronutrients at lower as well as at higher PPFD. This result was a reflection of the ability of those crops to produce higher shoot dry matter. Brazilian stylo produced the lowest shoot dry weight and was able to accumulate only minimal amounts of nutrients. The performances of joint vetch, crotalaria ochroleuca, showy crotalaria, and hairy indigo at both PPFD levels were all similar. All of these legumes improved their growth and micronutrient nutrient uptake at higher PPFD levels. Nutrient-use efficiency ratios of all the micronutrients studied were higher at 400 μmol m^{-2} s^{-1} PPFD than at 200 μmol m^{-2} s^{-1} PPFD. Increased PPFD improved nutrient-utilization efficiency. Inter-specific differences were observed for nutrient influx and transport. Maximum influx and transport were obtained for Mn and minimum values of these parameters were obtained for Cu. Regulation of light intensity by appropriate shade and soil micronutrient management appear to be critical in a plantation system to achieve the maximum potential benefits of cover crops.

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